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USES OF THE GROSS ANNUAL REPRODUCTIVE RATE CALCULATION IN THE SPOTTED DOLPHIN ASSESSMENT

by

Daniel Goodman

ADMINISTRATIVE REPORT LJ-84-22C

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Uses of the Gross Annual Reproductive Rate Calculation in the Spotted Dolphin Assessment

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June 1984

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$$u(x) = u_j e^{-a_j x} + u_c + u_s e^{a_s x}.$$

The parameters u_c, a_j, and a_s were set at 0.07, 0.184 and 0.184 respectively, and the natural rate of increase of the exploited population was set at 0.05. Bias was expressed as the discrepancy between the true value and the estimate divided by the estimate..... 12

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ABSTRACT

The gross annual reproductive rate (GARR) is a population statistic which theoretically represents a convolution of the age specific schedule of fecundity with the age distribution (though it is estimated from other data). Owing to the involvement of the age distribution in the statistic, problems may arise in applying the GARR measured in one population to another population with a different age distribution.

In dolphin assessment, there is a temptation to use the GARR for an unexploited population (where birth rate is assumed to balance death rate) to estimate mean per capita natural mortality, which is then compared to the GARR for a harvested population, in order to obtain an estimate for the natural rate of population increase in the harvested population. This procedure introduces an error, in that, though the GARR of the unexploited population is a legitimate estimate of the mean per capita mortality rate of that population, this statistic does not apply to the harvested population because the two have different age distributions (even if the two have identical natural mortality schedules, and the harvest is unselective).

The extent of the discrepancy will depend on the degree of age dependence of the mortality schedule and on the magnitude of the natural rate of increase in the harvested population.

I. INTRODUCTION

The gross annual reproductive rate (GARR) is a statistic representing the birth rate per capita of a defined segment of a population. There are various usages, differing with respect to the segment of the population that constitutes the basis for the statistic, and differing with respect to the measure of fecundity that defines the birth rate. A spectrum of such statistics, applied to cetacean population dynamics, is reviewed in Perrin and Reilly (1984).

In stock status assessment of the northern offshore spotted dolphin (Smith, 1979), use has been made of a GARR estimate obtained by dividing an estimate of the fraction of the population pregnant by an estimate of the gestation period (Perrin, Coe and Zweifel, 1976; Smith, 1983). In dynamical applications, GARR has been taken to represent a crude population birth rate, which could be used to estimate the population growth rate, if a crude population mortality rate were subtracted from it.

Specifically, the assumption has been made that in a population at replacement (an unharvested equilibrium population), where the population birth rate must equal the population death rate, the associated estimate of GARR could be taken as an estimate of the natural population death rate, which might then be used with an estimate of GARR from a harvested population to determine the natural rate of increase of the harvested population.

There are two distinct questions arising in connection with this application of GARR: (1) Does the measured quantity, fraction pregnant divided by the gestation period, actually estimate a mean per capita

population birth rate? (2) Can the GARR measurements from harvested and unharvested populations be combined in such a way to yield an estimate of population growth rate?

The answers to both questions are "no." For the first question, of estimating a fecundity rate from observations of fraction pregnant and duration of pregnancy, it turns out that even though the traditional GARR ratio is incorrect for this application, there is a correct mathematical expression for operating on pregnancy frequency and gestation time data to yield a proper fecundity estimate once mortality rates are also taken into account (Goodman, 1983b).

For the second question, of combining GARR measurements from harvested and unharvested populations, it likewise turns out that the underlying error cannot be corrected without knowledge of the actual natural mortality schedule in the harvested population. Since the absence of direct data bearing on the natural mortality rate was the motivation for this strategy of calculation based on GARR, there appears to be an impasse. The purpose of this paper is to describe the theoretical foundations of the impasse.

The notation and theory used in this paper are drawn from a more extensive treatment of collapsed parameter models for life history analysis (Goodman, 1983a).

II. MATHEMATICAL ANALYSIS

A special case of age independent parametrization occurs in the estimates of gross annual reproductive rate (GARR), obtained from observations of the frequency of pregnant individuals in the entire population and estimates of the duration of pregnancy or the duration of the interbrood interval. In particular, estimates of this sort have been used to calculate population growth rates for the eastern Pacific dolphin stocks. The calculations involve observations on harvested and unharvested stocks, and they further involve assumptions about the nature of the response of the life history to the reduction in population density resulting from harvesting. The assumptions are reasonable, but the method of combining observations from harvested and unharvested populations commits an error which generally will result in an upward bias in the resulting calculated population growth rate. The error cannot be corrected without age specific information on mortality (survival rates). The nature of the error will be explained in this section.

In this derivation we will use the continuous time description of the life history to represent the underlying life history, as this will greatly simplify the disentangling of the effects of harvest from the intrinsic life history. In the discrete time model, the fecundity rates, m, refer to effective fecundity, which includes an effect of mortality rates of the parents between the time of prior census and the birth event and an effect of mortality rates of offspring between the time of birth and first census. Since the harvest is, in effect, an increase in the mortality rates, the fecundity parameters in the discrete time model must include an effect of harvest, requiring, in particular, further assumptions about the relative timing of the harvest season and the reproductive season. In the discrete time model, likewise, we would need to know the actual timing of natural

mortality and harvest mortality, during the course of the finite time interval, so as to represent correctly the contribution of harvest mortality to total mortality. In the continuous time model, since we are dealing with instantaneous rates which are assumed to be time invariant, we do not have these complications.

For a variety of reasons, the discrete time model with annual time step actually is the more appropriate model for most real populations. Thus, in an actual parametrization of a harvested population, we would be obliged to deal with these complications of incorporating the effects of harvest mortality into the discrete time fecundity and survival parameters. In an actual application, we would also need to consider, in greater depth, the significance and duration of parental care, since this mechanism results in a compounding of the effect of harvest mortality on survival of young. However, since the present section is concerned only with a theoretical point, we will proceed with the continuous time notation, with which that point can be presented with greater clarity.

In the continuous time notation, denoted with the age subscripts enclosed in parentheses, $m(x)$ refers to the per capita age specific instantaneous birth rate, $u(x)$ refers to the per capita age specific instantaneous mortality rate, $c(x)$ refers to the differential representing the fraction of the stable population in the infinitesimal age category x, and r refers to the ultimate per capita instantaneous growth rate of the population. In this notation:

$$l(x) = e^{-\int_0^x u(y)dy} \qquad [1]$$

$$\int_0^w e^{-rx} l(x)m(x)dx = 1 \qquad [2]$$

and

$$c(x)dx = \frac{e^{-rx} l(x)dx}{\int_0^w e^{-ry} l(y)dy} \qquad [3]$$

For purposes of this derivation, then, we will treat GARR as identical with mean per capita birth rate of the population. In practice, GARR is used in discrete time applications, where it is treated, in principle, as identical to the mean per capita effective fecundity. Observations of pregnancy rates, or even tallies of birth events, are not actually sufficient for a correct discrete time estimate of GARR, owing to the convolutions necessary in converting from instantaneous events to the discrete time parameters, but this is a moot issue here, since the point of this section is that the fundamental premise of the dynamical use of GARR for estimate natural growth rate in a harvested population is in any case incorrect.

An age independent parametrization (Goodman, 1983a), in the continuous time notation, represents the dynamics in terms of a mean per capita instantaneous birth rate $\bar{m}$ and a mean per capita instantaneous mortality rate $\bar{u}$, obtained as

$$\bar{m} = \int_0^w c(x)m(x)dx \qquad [4]$$

$$\bar{u} = \int_0^w c(x)u(x)dx \qquad [5]$$

yielding

$$r = \bar{m} - \bar{u} \qquad [6]$$

which have their obvious analogs in the discrete time notation.

We are concerned here with three underlying life histories. The notation without prime superscripts will designate the life history of the unharvested population. The life history realized under the harvest, including the effects of the harvest itself, will be designated with a single prime superscript. The intrinsic life history of the harvested population, which is the life history of the harvested population where the contribution of the harvest has been removed, will be designated with a double prime superscript.

The difference between the intrinsic life history of the harvested population and the life history of the unharvested population is attributed to the lower population density, resulting from the harvest, in the harvested population. The natural mortality rates are assumed to be unaffected by density, so that

$$u(x) = (u'(x) - h) = u''(x) \qquad [7]$$

where h is the per capita instantaneous harvest rate, which is assumed to be time invariant and unselective with respect to age.

The harvest is assumed not to affect fecundity rates directly, but the lower population density associated with the harvest is assumed to result in a higher fecundity, so that

$$m(x) < m'(x) = m''(x) \qquad [8]$$

The intention in obtaining estimates of GARR is to employ these in calculations of population growth rate. In particular, there is a desire to compute the "natural" rate of increase of the exploited population. This is

r", the growth rate that the population would exhibit if it were instantaneously released from harvest.

The conventional formula employed obtains r" as the difference between the GARR of the exploited and unexploited populations, as per equation (6)

$$r'' = GARR' - GARR \qquad [9]$$

The belief is that GARR' represents the mean per capita birth rate in the exploited population and that GARR represents the mean per capita mortality rate in the unexploited population, and that both these rates apply to the released population, so the question reduces to whether we can define observable GARRs in such a way that

$$\bar{m}'' \overset{?}{=} GARR' \qquad [10]$$

and

$$\bar{u}'' \overset{?}{=} GARR \qquad [11]$$

given our assumptions encapsulated in equations (7) and (8).

Obviously, the identities needed in equations (10) and (11) will depend on the age distributions in the two observed populations. In particular, they will require that both the populations have age distributions identical to the hypothetical released population.

This will give no difficulty for identity (10) since the released and the exploited populations differ only in their mortality rates, and that difference is owing to the age independent increment attributable to the harvest. There is a theorem, which will be recapitulated in detail below, that this sort of across-the-board modification of mortality rates does not affect the stable age distribution, so we will have it that c"(x) equals c'(x).

On the other hand, identity (11) requires that the released and the unexploited populations have the same age distribution. But these respective populations have the same mortality schedules, while, owing to the presumed density response of fecundity, they will not have identical growth rates. Under these conditions, their stable age distributions must differ, making (11) impossible, as will be shown below.

Equation (10) is easily satisfied. With GARR' defined as the mean per capita fecundity observed in the exploited population:

$$GARR' = \int_0^w c'(x)m'(x)dx \qquad [12]$$

From equations (1) and (7)

$$l'(x) = l(x)e^{-hx} \qquad [13]$$

and

$$l''(x) = l(x) \qquad [14]$$

From equation (2)

$$\int_0^w e^{-r'x} l'(x)m'(x)dx = 1 \qquad [15]$$

and

$$\int_0^w e^{-r''x} l''(x)m''(x)dx = 1 \qquad [16]$$

From (13), equation (15) becomes

$$\int_0^w e^{-r'x} l(x)e^{-hx}m'(x)dx = \int_0^w e^{-(r'+h)x} l(x)m'(x)dx = 1 \qquad [17]$$

From (14) and (8), equation (16) becomes

$$\int_0^w e^{-r''x} l(x)m'(x)dx = 1 \qquad [18]$$

Equations (17) and (18) are identical except for the expressions in the exponent. Since both equations have the same value, the exponents must be equal, thus

$$r'' = r' + h \qquad [19]$$

From equation (3)

$$c'(x) = \frac{e^{-r'x}\, l'(x)}{\int_0^w e^{-r'y}\, l'(y)dy} \qquad [20]$$

and

$$c''(x) = \frac{e^{-r''x}\, l''(x)}{\int_0^w e^{-r''y}\, l''(y)dy} \qquad [21]$$

Substituting (13) into equation (20)

$$c'(x) = \frac{e^{-r'x}\, l(x)e^{-hx}}{\int_0^w e^{-r'y}\, l(y)e^{-hy}dy}$$

$$= \frac{e^{-(r'+h)x}\, l(x)}{\int_0^w e^{-(r'+h)}\, l(y)dy} \qquad [22]$$

Substituting (14) and (19) into equation (21)

$$c''(x) = \frac{e^{-(r'+h)x}\, l(x)}{\int_0^w e^{-(r'+h)y}\, l(y)dy} \qquad [23]$$

From (22) and (23)

$$c'(x) = c''(x) \qquad [24]$$

Substituting (8) and (24) into equation (12)

$$GARR' = \int_0^w c''(x)m''(x)dx$$

$$= \bar{m}'' \qquad [25]$$

thus satisfying (10).

By analogy with (12)

$$GARR = \int_0^w c(x)m(x)dx \qquad [26]$$

Assuming that the unexploited population is at equilibrium, with zero population growth, its mean per capita birth rate must balance its mean per capita mortality rate, so that, from (26)

$$GARR = \bar{u} \qquad [27]$$

From (5) and (7), then,

$$GARR = \int_0^w c(x)u''(x)dx \qquad [28]$$

Substituting (14) in equation (16), and recalling equation (2)

$$\int_0^w e^{-r''x} l(x)m''(x)dx = 1$$

$$= \int_0^w e^{-rx} l(x)m(x)dx \qquad [29]$$

From equation (8), we already have it that $m''(x)$ is greater than $m(x)$. Therefore, in comparing the integrals on both sides of equation (29), which must have the same value, we see that: each has the same element $l(x)$ in the

integrand; m"(x) and m(x), which appear in the respective integrands, are related by (8); so, to achieve equality, it must be the case that

$$r'' > r \qquad [30]$$

or

$$r'' = r + k \qquad [31]$$

where k is some unknown positive value, reflecting the increase in the "natural" rate of increase owing to density dependence.

Given our assumption of zero growth in the unharvested population,

$$r = o \qquad [32]$$

and so

$$r'' = k \qquad [33]$$

Substituting (32) in equation (3)

$$c(x) = \frac{l(x)}{\int_0^w l(y)dy} \qquad [34]$$

Substituting (33) and (14) in equation (21)

$$c''(x) = \frac{e^{-kx} l(x)}{\int_0^w e^{-ky} l(y)dy} \qquad [35]$$

From (34) and (35)

$$c(x) = c''(x)e^{kx}\left[\frac{\int_0^w e^{-ky}\,l(y)\,dy}{\int_0^w l(y)\,dy}\right] \qquad [36]$$

Note that the term in square brackets in equation (36) is just a normalizing scale factor that does not depend on x. Let us simply designate this as []. Then, substituting (36) into equation (28)

$$GARR = \int_0^w c''(x)u''(x)e^{kx}[]\,dx$$

$$= []\int_0^w c''(x)u''(x)e^{kx}\,dx \qquad [37]$$

Clearly, unless k=0 or u(x)=constant, this value for GARR will not be equal to

$$\bar{u}'' = \int_0^w c''(x)u''(x)\,dx \qquad [38]$$

so equation (11) is not satisfied.

III. IMPLICATIONS, AND A NUMERICAL EXAMPLE

We have found that the GARR generally does not equal the natural mortality rate in the harvested population. Comparing equations (37) and (38), we see that the difference lies in the normalized term $e^{kx}[]$, which will weight the older age classes more heavily (i.e., this exponential weighting factor increases exponentially with age).

Generally, for biological reasons, the mortality rates of the youngest and oldest age classes will exceed those of adults in their prime. The relative impacts, on the mean per capita mortality rate, of these two deviations from constant mortality will depend on three factors: the magnitudes of these "juvenile" and "senescent" mortality components obviously are a consideration; the magnitude of the pre-senescent mortality components and the age at which the senescent mortality begins to be exerted will determine what fraction of the population is exposed to senescent mortality;

and the magnitude of the natural growth rate of the harvested population (k) will determine the slope of the curve that differentially weights the mortality rates of the respective age classes.

In a case where the effect of the juvenile mortality component dominates the effect of the senescent component (more individuals in the stable age population die from juvenile than senescent mortality), over-weighting the older age classes in the integral (37) will give a spuriously low value, for it will have under-represented the effect on the mean per capita mortality of the higher mortality rate of the younger age classes. Which is to say that, with this assumed pattern of mortality, GARR will invariably underestimate $\bar{u}$", and the quantity GARR' minus GARR will invariably overestimate the growth rate r".

By contrast, where the effects of senescent mortality dominate those of juvenile mortality, GARR will overestimate $\bar{u}$", and the quantity GARR' minus GARR will underestimate the growth rate r". And there must be a family of mortality schedules where juvenile mortality just balances senescent mortality in such a way that the GARR calculation, for this special case, is unbiased.

Siler (1979) proposed parametrizing the age specificity of the mortality schedule in terms of explicit "juvenile," "constant" and "senescent" components. His equation is

$$u(x) = u_j e^{-a_j x} + u_c + u_s e^{a_s x} \qquad [39]$$

where u_j is the initial magnitude of the juvenile mortality component, which decays exponentially with age according to the coefficient a_j, u_c is the constant mortality component, and u_s is the initial magnitude of the senescent mortality component, which increases exponentially with age according to the coefficient a_s. In practice, this 5-parameter model offers vast mathematical flexibility relative to the plausible shapes of real mortality schedules, so for those few cases where the shape of the mortality schedule is known in some detail, a very good fit is readily achieved.

As an illustration, we consider the family of mortality schedules described by equation (39) where the value of u_c is 0.07, and the values of a_j and a_s are both 0.184. With these parameter values, the constant mortality component alone will account for the death of 99.9% of the individuals before the age of 100, the juvenile mortality component decays to 1% of its initial value by age 25, and the senescent mortality component is initially 1% of the value it reaches by age 25.

Figure 1 shows the bias in the value of the growth rate r" estimated from the GARR' minus GARR procedure, where the actual value of r" is 0.05, and initial magnitudes of the juvenile and senescent mortality components, u_j and u_s respectively, are given by the y and x axes, and the rest of the parameters are fixed at the values described above. As explained qualitatively, the bias in the estimated r" is positive when the effect of juvenile mortality is strong relative to that of senescent mortality, and it is negative when the converse holds.

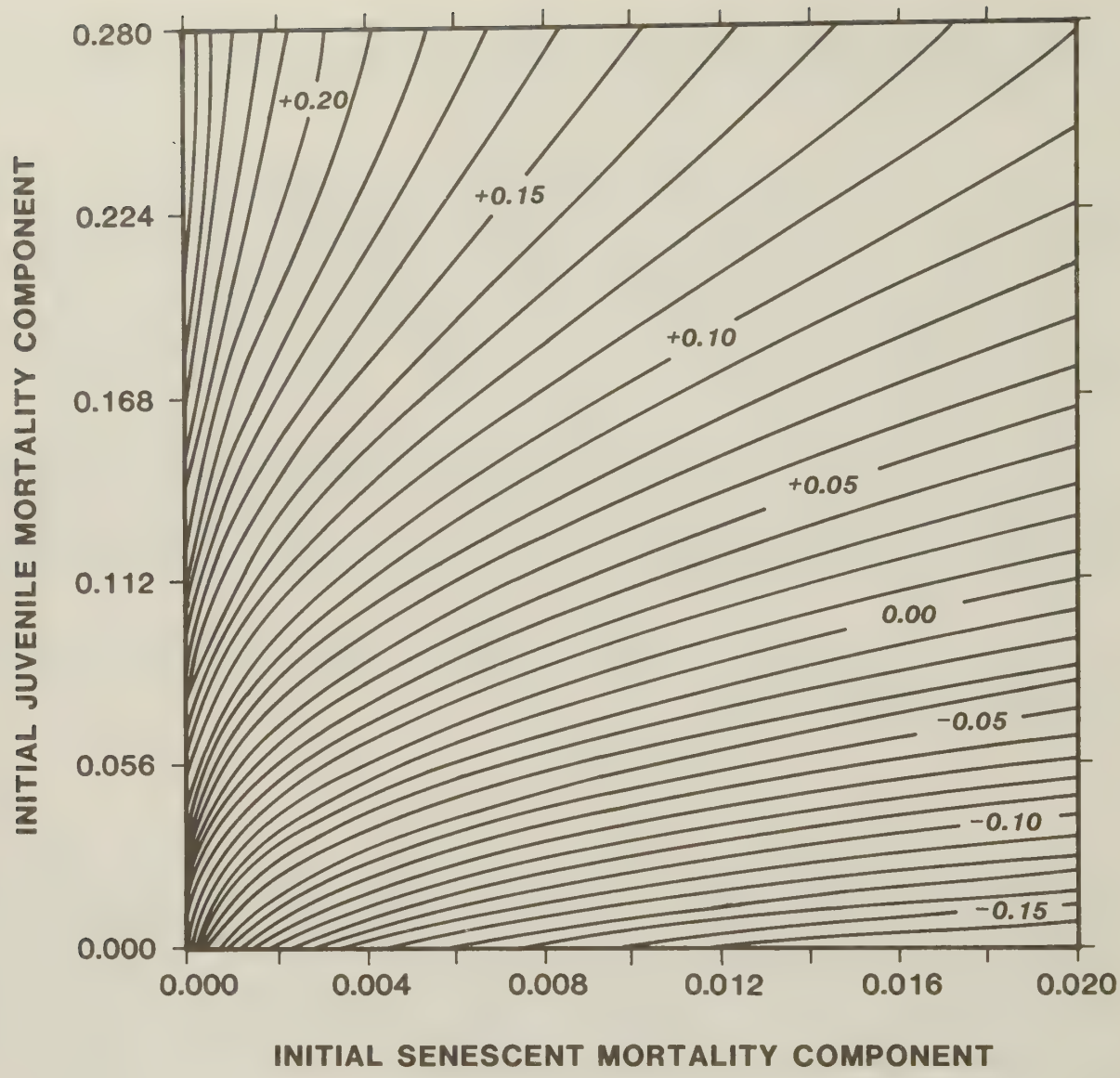

Figure 1. Contour plot of bias in the estimate of natural growth rate obtained from subtracting the GARR of an unexploited population at equilibrium from the GARR of an exploited population at stable age distribution under an unselective harvest. The axes of the plot are two parameters u_j and u_s, referring to the initial values of the juvenile and senescent mortality components in a mortality schedule parametrized according to the model

$$u(x) = u_j e^{-a_j x} + u_c + u_s e^{a_s x}.$$

The parameters u_c, a_j, and a_s were set at 0.07, 0.184 and 0.184 respectively, and the natural rate of increase of the exploited population was set at 0.05. Bias was expressed as the discrepancy between the true value and the estimate divided by the estimate.

Barlow (1984) has proposed calibrating the senescent mortality component of the northern offshore spotted dolphin population in terms of the maximum longevity detectable in modest samples of individuals with a mortality schedule following equation (39). One such calibration, using optimistic (i.e., low) values for the juvenile mortality component (concerning which relevant data are not available) was tabulated using 40 years as the presumed age at 5% survivorship. In Table 1, we show such a tabulation, modified from Barlow's values only for the last age classes (45 and 46) so as to avoid the implications of an infinite continuous time mortality rate in a life table that was truncated at age 45.

The biases resulting in the GARR' minus GARR estimate of r" for this presumed dolphin survivorship schedule are listed in Table 2, for a variety of values of the true magnitude of r". Barlow (1984) suggests that 0.041 might be a reasonable upper limit for r", in which case the bias in the estimate will be approximately -15%, provided we accept the assumption that the harvest is unselective. This bias is not trivial in magnitude, but it is small compared to the effects of other known erroneous assumptions and questionable features of the dolphin data.

IV. SUMMARY

We have found that the GARR estimated for an unexploited population at replacement is not a correct estimate of the natural mortality rate in the corresponding harvested population, even with the best case assumption of unselective harvest and identical schedules of natural mortality. Therefore, an estimate of natural growth rate, based on the difference between the GARRs of the harvested and unharvested populations, will be in error.

Therefore, even if we come to an appropriate set of formulae for calculating GARR' and GARR from trustworthy discrete time data, this still will not provide an unbiased estimate of r", the "natural" growth rate which is the object of our interest. Since r" is equal to k, which itself is the exponent of the exponential distortion which is causing the bias, we have no way of making assumptions about the magnitude of the bias without concommitantly making assumptions about the magnitude of r", which of course begs the question.

This suggests an iterative approach to the problem, adjusting an exponential correction in GARR until the difference between GARR' and the "corrected GARR" converges on the exponent of the correction. Unfortunately, the correction is not a simple factor applied to the uncorrected GARR; instead it involves a convolution of the exponential with the schedule of age specific mortalities u(x). So, we cannot correct the bias in the calculation without recourse to age specific information.

If we confined our GARR calculation to the adult segment of the population and were assured that the mortality rates of all adults are the same (regardless of age), this adult GARR would not be subject to the age distribution distortion. However, this adult GARR could not be used directly for computing r" as a simple difference. In particular, it would be necessary to know the true age of maturity and the survival to maturity in the exploited

Table 1. Model survivorship schedule, adapted from Barlow (1984).

AGE CLASS	SURVIVAL-RATE (DISCRETE)	SURVIVORSHIP (DISCRETE)	MORTALITY-RATE (CONTINUOUS)
(1)	.85000	1.00000	.16252
(2)	.90000	.85000	.10536
(3)	.98500	.76500	.01511
(4)	.98500	.75352	.01511
(5)	.98500	.74222	.01511
(6)	.98500	.73109	.01511
(7)	.98500	.72012	.01511
(8)	.98500	.70932	.01511
(9)	.98500	.69868	.01511
(10)	.98500	.68820	.01511
(11)	.98500	.67788	.01511
(12)	.98500	.66771	.01511
(13)	.98500	.65769	.01511
(14)	.98300	.64783	.01714
(15)	.98200	.63681	.01816
(16)	.98000	.62535	.02020
(17)	.97900	.61285	.02122
(18)	.97700	.59998	.02326
(19)	.97500	.58618	.02532
(20)	.97300	.57152	.02737
(21)	.97000	.55609	.03046
(22)	.96700	.53941	.03355
(23)	.96400	.52161	.03666
(24)	.96000	.50283	.04082
(25)	.95500	.48272	.04604
(26)	.95000	.46099	.05129
(27)	.94400	.43794	.05762
(28)	.93700	.41342	.06507
(29)	.92900	.38737	.07364
(30)	.92000	.35987	.08338
(31)	.91000	.33108	.09431
(32)	.98900	.30128	.01106
(33)	.88500	.29797	.12217
(34)	.87000	.26370	.13926
(35)	.85300	.22942	.15899
(36)	.83400	.19570	.18152
(37)	.81300	.16321	.20702
(38)	.78900	.13269	.23699
(39)	.76300	.10469	.27050
(40)	.73400	.07988	.30925
(41)	.70200	.05863	.35382
(42)	.66700	.04116	.40496
(43)	.63200	.02745	.45887
(44)	.59000	.01735	.52763
(45)	.00010	.01024	9.21034
(46)	.00010	.00000	9.21034

Table 2. Computed values of the mean per capita natural mortality rate in the exploited population, and fractional error in an estimate of the natural rate of increase obtained by subtracting GARR for the unexploited population (0.04915) from the GARR of the exploited population, using the model schedule of mortality rates from Table 1, for various values of r, the natural growth rate (per capita production) of the exploited population.

r	MEAN MORTALITY	ERROR IN r
0.000	.04915	0.00000
.005	.04799	-.30346
.010	.04698	-.27802
.015	.04611	-.25416
.020	.04539	-.23182
.025	.04480	-.21089
.030	.04433	-.19132
.035	.04399	-.17301
.040	.04376	-.15589
.045	.04363	-.13990
.050	.04360	-.12495
.055	.04366	-.11099
.060	.04380	-.09795
.065	.04402	-.08577
.070	.04430	-.07440

and unexploited populations, since we would be using the GARR so calculated as a fecundity parameter in a geometric series parametrization.

We conclude that calculating the natural rate of increase of a harvested population by subtracting from an estimate of its mean per capita fecundity an estimate of the mean per capita mortality in a corresponding unharvested population at equilibrium will introduce possibly substantial errors which cannot be corrected without information on the age dependence of the mortality schedule. Numerical investigation of the likely magnitude of the bias for mortality schedules and population growth rates appropriate for many marine mammals indicates that the bias is probably of an order that is less than other likely sources of error, though it is not negligible in itself.

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